Epilogue

Drent, R.H.

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Although the papers presented here do not have the pretension of exhaustively reviewing the adaptations enabling survival through the polar winter, the range of organisms covered nevertheless allows one to discern recurring themes. For the endotherms it is tempting to set the current views against the background of the generalizations arrived at by Scholander and his co-workers (Scholander *et al.*, 1950) in their key papers cited repeatedly during the Life in the Polar Winter conference. We can ask why the paradigm of Newtonian cooling advanced at that time has been such a successful approach to the problem of cold adaptation and to what extent the conclusions based on the wide-ranging survey undertaken then are still valid today.

The simple physical model (Newtonian cooling) employed by the Scholander team had the great virtue of reducing the characterization of physiological adaptations to a small set of values (conductance, resting metabolic rate, the lower critical temperature and core body temperature), allowing prediction of cost at defined ambient conditions. More important, species could be readily compared using these basic measurements, which could be achieved using modest resources during relatively short-term trials with animals brought in from the wild.

The basic tenet of the Scholander view was that adaptation to arctic life primarily entailed the acquisition (or perfection) of effective insulation, thus allowing cold exposure without excessive costs. This basic realization has been brought home dramatically by empirical measurements presented at this symposium and is exemplified by the small arctic fox, whose pelage thickness is the most effective insulator known. Although these measurements confirm the utility of using fox furs for caps, hit upon by trial and error by the earliest Europeans to winter in the polar regions, it is difficult for us (as transplants from a tropical pedigree) to appreciate that these small mammals can withstand temperatures down to -25°C without shivering, indeed without added metabolic cost.

The metabolic savings are complemented by an absolute economy in exposure to the elements. The smaller arctic endotherms demonstrate a mastery in exploiting shelter, and indeed the winter biology of the ringed seal is intimately bound up with the utilization of chambers under the sea ice. Presence of suitable shelters defines local distribution of the arctic fox, and survival through the harsh winters of northeast Asia, with temperatures of -40°C, is feasible for willow ptarmigan because they shelter beneath the snow and venture to the surface for only brief foraging forays.

The accumulation of fat deposits as an emergency supply in the ensuing winter has been explored quantitatively in several species. In ptarmigan and the arctic fox these supplies suffice as an emergency supply only, and the detailed work reported in Oritsland (1986) points to a similar role for fat in reindeer, sufficient only to bridge catastrophic conditions during the Spitsbergen winter. These findings imply that overwinter survival cannot be assured simply by anticipatory energy accumulation but must depend primarily on the ability to maintain a balance between intake and expenditure throughout. In some species (notably the arctic fox) an additional buffer in the form of cached food can be drawn upon when hunting conditions are unfavourable.

The ultimate economy is entailed by lowering of locomotor activity, often hand in hand with the use of shelters alluded to earlier when discussing Andreev's work on the willow ptarmigan. In the related rock ptarmigan, Mortensen and Blix (1989) found that when birds caught on Spitsbergen were maintained in outdoor enclosures in arctic Norway, food consumption at midwinter was in fact only half that during summer, and these workers surmised that changes in activity costs accounted for part of these savings. In the wild, the necessity of economizing during winter is emphasized by the dramatic fall in food quality available for browse (willow ptarmigan, see Brittas, 1988).

The salient features enabling successful wintering by man (use of shelter, food caches, effective clothing with high but adjustable insulative value and avoidance of excessive expenditure) are thus themes recurring among the wild fauna. Apparently the use of external heat (fire) is the only feature unique to man. The ultimate reliance on cached food is vividly brought to mind by Richardson's account of the return of Franklin's exploring party to the arctic coast of central Canada in the fall of 1822. The caloric budgets worked out by Houston (1984) make it clear that a successful crossing of the area appropriately known as the barrens at this time of year was only possible by boiling moccasins and caribou hides left behind from a previous winter camp.

The need for avoidance strategies was thus early appreciated but only recently has their effectiveness been quantified. Features requiring redoubled attention include the scope of energy savings incurred during prolonged starvation by lowering the metabolic rate, an adaptation emphasized in discussing survival of the arctic fox under inhospitable conditions. The fact that hibernation as an escape strategy is available to only few members of the arctic fauna was also brought up during the conference. The impressive ability of arctic fauna to cope with the polar winter must not blind us to the fact that from time to time a combination of extreme cold and unfavourable feeding conditions leads to an exhaustion of the short-term bridging fat supply and massive mortality may result (see Oritsland, 1986, for documentation).

These observations imply that carrying these emergency supplies has a very real cost (indeed some 15% of current energy expenditure in the rock ptarmigan, according to Mortensen and Blix, 1989) and that only "average" interruptions in the food supply can be accommodated. The disaster years familiar to anyone working in the Arctic — exemplified by near total failure of reproduction in the hardy Svalbard reindeer, coupled with heavy overwinter mortality of the adult animals (80% starvation) — emphasize that the challenge of arctic survival resides not only in surmounting extreme cold but in withstanding an unpredictable variance in conditions. In the economy of survival the margins are narrow.

The vivid accounts of ongoing research presented during the symposium and in this issue underline the shifting emphasis away from relatively short-term incursions to the arctic environment to capture specimens for subsequent study towards long-term work by teams of investigators following individual animals over long periods (maintaining contact by an impressive array of telemetric devices). The challenge of the years ahead will be to trace the web of adaptation through the food chain by close collaboration among specialists. In the case of herbivory, cooperation between botanists and zoologists alluded to by Sonesson has already revealed the intimate links connecting animal numbers with their food supply and especially with the persistence of the preferred vegetation (see also Jefferies, 1988). The close fit between the overall standing crop of vegetation and peak reindeer biomass across a range of arctic sites, even extrapolating to an accurate prediction of the carrying capacity of the sub-Antarctic island South Georgia, argues for the pervasive influence of food supply as against the traditional interpretation of populations kept in check by predators (Leader-Williams, 1988). It is against this background that the exploitation patterns of man must be viewed. From the recent physiological work undertaken on the members of the Finnish polar expedition, it is reassuring to note that urban man has not lost the ability to acclimatize to the dramatic extent envisaged by Hammel (1964), and more surprises may be in store for us.

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R.H. Drent
Biology Centre
University of Groningen
Groningen, The Netherlands